RECENT CONTRIBUTIONS TO THE KNOWLEDGE OF THE CRYSTALLINE STYLE OF LAMELLIBRANCHS.

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The crystalline style of pelecypod and of gastropod molluscs has long been a fascinating subject for investigation by students of these groups. In a paper (Nelson, '18) published six years ago the attempt was made to summarize and to analyse the more important contributions which had appeared up to that time, and by original observation to solve some of the problems regarding the origin, nature, and function of this structure. The conclusions of Coupin, '00, Mitra, '01, and others, that the crystalline style contains strong amylolytic ferments, were confirmed. In addition the style was shown to have at least two other functions. The first and more important of these is the rôle played by the style in the separation of food materials from sand and other waste. The powerful cilia of the style sac spin the style around on its long axis while pushing it anteriorly into the stomach. The head of the rotating style gathers the food strings coming from the œsophagus and as the whole mass is whirled around in the stomach much of the sand and other non-digestible matter is sorted out mechanically by the ciliary tracts of the stomach wall, and passed on into the intestine. At the point where the head of the revolving style comes into contact with the anterior wall of the stomach there is developed a tough resistant covering which I named the "gastric shield" (*flêche tricuspide* of Poli, 1791). The importance of such a sorting and stirring mechanism in animals in which ciliary activity has completely replaced muscular peristalsis, was pointed out.

In forms such as most of our common bivalves, where the style sac is incompletely separated from the intestine by two ridges or typhlosoles, an additional function is served. Food particles escaping from the stomach may be passed across the faces of the typhlosoles from the intestine and then be incorporated into the style. Most of such returned material enters the style sac near its base and is built into the soft core of the style. I have found oysters in which the entire core of the style was almost a solid brown mass of *Glenodinium*. In this position food materials at first rejected from the stomach in the separation of inert materials may be recovered as the style is moved gradually forward into the stomach.

In the interval since this paper, Nelson, *l. c.*, was published there have appeared several noteworthy contributions to the knowledge of the physiology of digestion in bivalve molluscs, and of the function of the crystalline style. It is well therefore to review these at this time and to give such additional information as has been accumulated during the past seven years in order that the present status of the problem of the crystalline style may readily be ascertained.

Edmondson ('20), in a detailed and very well illustrated paper, describes the reformation of the style of *Mya arenaria* following its extraction. Among the species of bivalves which occur on the northwest coast this investigator found in *Cardium corbis*, *Saxidomus giganteus*, *S. nuttallii*, and *Paphya staminea*, that starvation or removal from the water resulted in dissolution of the style "within a few days at most." In other species, notably *Siliqua patula*, *Schizothærus nuttallii*, *Macoma nasuta*, the style was found to be far more resistant to dissolution, being present even at death through starvation. In *Mya* only slight dissolution of the style occurred even after 14 days out of water. (Contrast this with the oyster, in which dissolution of the style occurs while the molluscs are exposed during the low tide; Nelson, '18.) As Edmondson points out, the forms with resistant styles possess a style sac nearly or completely separated from the intestine.

Experiments were performed with *Mya* in which the mantle was cut in the midline along the ventral surface for a distance of 15 to 25 mm. posterior to the pedal opening. A transverse cut was made near the middle of the style sac and the style extracted. The clams were then planted out and the rate of regeneration of the style studied. No food was taken apparently until the style was sufficiently regenerated to project into the stomach, from which Edmondson concludes that ingestion and digestion of food depend upon the degree of development of the crystalline style. A period of approximately 74 days were required for complete reformation of the style following the extraction.

This part of Edmondson's work and the conclusions he draws from it are open to some objection. As the experiments were carried out, there is no way of distinguishing the time actually required for style regeneration from the period of inactivity resulting from the effects of the operation. Out of 147 clams operated upon of which the observation period was in excess of three weeks, only 61, or approximately 42 per cent, survived the operation. Any operative procedure which results in the death of over one half of the animals should be carefully checked before conclusions are drawn from the results, and it seems that such checks were not made. The cut through the mantle alone must seriously have interfered with feeding. Bivalve molluscs are very sensitive to injury and will "sulk" without feeding for long periods after even slight disturbances.

A much better method of determining the period required for regeneration of the crystalline style would seem to be to determine the rate at which this structure is pushed forward into the stomach and dissolved during the normal feeding of the mollusc. This may be determined readily in forms which like the oyster and fresh-water mussels have a style sac incompletely separated from

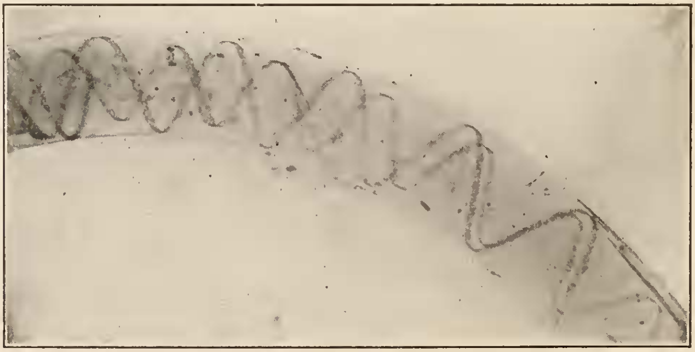

FIG. 1. The crystalline style of *Lampsilis luteola* taken from an individual which had been allowed to siphon in water containing a suspension of fine carmine grains. The spiral bands are composed of carmine which was caught upon the gills, carried into the stomach, thence to the intestine from which it was fed across the typhlosoles at two points near the anterior end of the style sac and incorporated into the style.

the intestine. A weak suspension of finely divided carmine if added to a water rich in food materials will usually be ingested along with the food and may be incorporated into the style. In some instances the carmine is passed across the typhlosoles into the base of the style sac and results in a red style. In others, the carmine may be fed into the style sac at some point between the stomach and the base of the sac, in which case the carmine forms a spiral band about the style as it is rotated and pushed anteriorly, giving the effect of a barber's pole (Fig. 1). Allen ('21) records a similar observation in a fresh-water mussel where minute green organisms took the place of the carmine.[1]

Complete regeneration of the crystalline style in *Ostrea*, *Modiolus*, *Anodonta*, and *Lampsilis* will take place at summer temperatures in from approximately 15 minutes in the oyster to a few hours in the other genera. Allen ('21) finds style regeneration in fresh-water mussels in about 24 hours. It is difficult to believe that a process which occurs in at the most a few hours in many of our common bivalves should require two and a half months in an active rapidly growing mollusc such as *Mya*. Although I have had no experience with this form, it would seem possible to inject by means of a hypodermic syringe a small amount of carmine in sea water near the base of the style sac and to determine the speed at which this pigment, incorporated into the style, is carried toward the stomach. If carefully performed such an operation should be far less drastic in its effects than was the technique employed by Edmondson.

In their admirable work on the natural history and propagation of fresh-water mussels Coker and his associates ('21) accept the conclusions of my 1918 paper, but contribute no original observations regarding the function of the crystalline style. Included in the former paper, pp. 88–91, are the observations of Dr. Franz

[1] While this paper was in press I received a copy of the report of Dr. J. H. Orton '24 on the causes of unusual mortality among oysters on English oyster beds; Ministry of Agriculture and Fisheries, London. On page 54 of this report is figured the crystalline style of *Ostrea edulis*, bearing a spiral band of food organisms. In a footnote on the same page this author suggests that one function of the style is "the mechanical one of drawing the mucous strings enveloping the food material into the stomach by twisting the strings around the shredded revolving head of the style like a capstan." In my 1918 paper, pg. 101, it is observed that "so strong is the tractive force of the rotating style that strings of mucus from any part of the body if led to the stomach cavity, are at once drawn in and wound up in the food mass."

Schrader on the food of mussels. This investigator found that only about one half of the diatoms and green algæ taken in were digested, and he concluded that these organisms play a comparatively unimportant rôle in the food supply of mussels. He apparently was unaware that in the process of sorting over of the acquired food materials by the ciliary tracts of the stomach, aided by the rotation of the crystalline style, many food organisms are shunted off into the intestine along with the sand and dirt. Especially may this be true of relatively heavy forms such as the diatoms. Some of these escaped food organisms may be passed across the typhlosole into the style sac and thus eventually be returned to the stomach, but a considerable number escape undigested from the anus. Blegvad '15 likewise draws false deductions as to the "insignificant" rôle played by plankton organisms in nutrition, from the finding of living planktonts in the fæces of the European oyster.

While at Madison, Wisconsin, I kept *Anodonta* and *Lampsilis* for months at a time in clear running water in which the chief food supply consisted of desmids, diatoms, and nannoplankton forms most of which were growing upon the sides of the tank and upon the shells of the mussels themselves (Allen, '14). Examination of the intestinal contents revealed many living organisms but also the empty tests of numerous diatoms which had been digested. Imperfect as may be the mode of separation of food from dirt by the ciliary mechanisms within the alimentary canal of bivalves, the wonder is that it functions as efficiently as it does. Such living organisms as are cast out in the fæces are not altogether lost since they accumulate on the shells or upon nearby objects, where they multiply rapidly within the fæcal remains and form a rich growth which is continually contributing its quota of food to the siphons of the mollusc (Allen, '14; Martin, '23).

Allen ('21) gives a detailed account of experiments on the effects of various food organisms in the formation of the crystalline style of fresh-water mussels. The details of this work cannot be discussed here, but in general they confirm and extend the findings of his preliminary paper (Allen, '14) and my own conclusions (Nelson, '18) regarding the rôle of food in style regeneration. He further showed that nannoplankton is relatively more effective than is net plankton in effecting style formation.

The only essential difference between Allen's results and mine is that in fresh-water mussels he found that relatively little escaped food was fed back into the stomach by way of the style, and he concluded that this reclaiming function of the style was of relatively little importance in these animals. The largest amounts of such material were found in the core of the style soon after regeneration of a new style had begun, an observation which I can confirm in *Anodonta grandis*. The relative efficiency of this retrieving mechanism in various bivalves will have to be extensively studied before we shall be in a position to determine its importance to molluscs generally. The fact that *Mya*, *Teredo*, *Martesia* and many other genera with a style sac nearly or quite separated from the intestine are able to exist without such a mechanism indicates that on the whole it plays perhaps a minor rôle in nutrition. Phylogenetically it probably represents the development of a strong recurrent tract of cilia situated in the posterior part of the stomach of the ancestors of present-day types; such a group of cilia as may, for example, be demonstrated in the stomach of the larval oyster.

Allen (*l. c.*) lays still further emphasis upon his conclusion of 1914, voiced likewise in my 1918 paper, that the crystalline style arises in response to the presence of food in the stomach. Evidence that such may not be the case is discussed further on in connection with the findings of Berkeley ('23).

Nogouchi '21 examined the crystalline styles of various marine bivalves and gastropods for *Cristispira*, a large active spirochæte which was first discovered in the style of the oyster. The spirochætes were found most frequently in *Ostrea*, next in *Mya*, then in *Modiolus;* but not at all in *Venus*, *Ensis*, *Mactra*, *Mytilus*, *Pecten*, *Fulgur*, and *Nassa*. Gross, however, has reported *Cristispira pectenis* from the crystalline style of *Pecten*. Nogouchi did not know of my 1918 paper in which is discussed briefly the occurrence of *Cristispira* in the styles of certain bivalves and its absence from others. Nogouchi observed that the style of the oyster quickly liquefied after extraction from the body, and that only oysters freshly removed from natural conditions contained this structure. He believes that the great abundance of *C. balbiani* in the oyster is due to the relatively soft consistency of the style in this mollusc, and that the absence of spirochætes in many molluscs is due to the very firm and resistant styles which they possess.

Although the solidity and resistance to dissolution of the style may effect the distribution of *Cristispira*, they are certainly not the most important factors. As Nogouchi himself admits, and as Edmondson showed, the style of *Mya* is very firm and relatively resistant to dissolution, yet it harbors *Cristispira* in an abundance second only to that of *Ostrea*.

Martin ('23), studying the relative importance of the net plankton and of nannoplankton in the food of the oyster, found that water from which even the smallest nannoplankton organisms including bacteria had been removed would, if well aërated, permit reformation of the style in *Ostrea*. He concluded that although the appearance of the style in this mollusc is usually correlated with the taking in of food, this structure may arise in the complete absence of food, presumably as a response to the act of siphoning.[1]

Three months after the publication of Martin's paper appeared an interesting communication from Berkeley ('23) regarding the function of the crystalline style as a possible factor in the anaërobic respiration of certain marine molluscs. This investigator attempts to account for the continued production of carbon dioxide by marine molluscs kept under anaërobic conditions, as demonstrated by Collip ('21). In seeking a possible explanation of this production of carbon dioxide Berkeley tested the reactions of various tissues and of the style of *Saxidomus* with an alcoholic solution of gum guaiacum. Only in the case of the style did he obtain a deep blue color, which suggested to him that this structure might be associated with anaërobic respiration. Molluscs kept under anaërobic conditions showed in all cases an absence of the style. In an earlier paper (Berkeley, '21) it was shown that a disappearance of glycogen accompanies anaërobiosis in *Saxidomus gigantea*, though not in *Paphia* nor in *Mya*.

It is pointed out in a footnote of Berkeley's ('23) paper that the work was done in ignorance of the publications of Mitra, Allen,

[1] Although an oyster has no siphons, this term has come into such general use for the process of passing water through the gills of a mollusc that it seems best to employ it here—especially as no good substitute appears to be available.

Nelson, and Edmondson, and that in the light of the findings of these and of other workers a more critical series of experiments is needed to determine the relative importance of food and of oxygen in determining style formation. Berkeley concludes that the presence or absence of the style depends upon the presence or absence of oxygen, and he makes the astonishing assumption that food plays no part in the building up of this structure, on the ground that oatmeal added to the water caused no regeneration of the style. No examinations were made to determine whether the animals were eating the oatmeal, nor were any tests made using the natural plankton food of the molluscs.

Taking the results of Martin and Berkeley together, however, I believe that Allen and I were mistaken in laying undue emphasis upon the rôle of food in stimulating style secretion. Although the presence of food in the stomach may play a part in the mechanism of style formation, Edmondson's finding that no food was taken by *Mya* until after the head of the regenerating style protruded into the stomach; Martin's results in obtaining style regeneration in aërated water devoid of all net and nannoplankton; and Berkeley's conclusion that no style forms under anaërobic conditions, all point to the probability that secretion of the crystalline style may be a direct response to siphoning, regardless of whether the incoming water contains food organisms or not.[1]

The chief criticism centers about the following conclusions of Berkeley; first, his assumption that since the style disappears when the bivalve is kept under anaërobic conditions it therefore represents a reserve of oxygen. As well might one conclude that all secretions contain reserve oxygen since secretion is diminished during decreased activity of the organism. Second, no correlation was shown between the size and persistence of the crystalline style on the one hand and the degree of aëration of the environment on the other. As bearing upon the first of these assumptions Gray, '23, showed that for ciliary movement the degree of mechanical activity exactly parallels the relative amount of oxygen absorbed. Since the formation and movement of the

[1] Orton, '24, l.c., pg. 55, observes that sound *O. edulis* will reform a style in the absence of food, but from the text it is not clear that all nannoplankton was removed from the water.

style are so largely dependent upon the activity of the powerful cilia of the style sac, it is to be expected that no style would form in an absence of oxygen. From what we know also regarding the oxygen consumption of the glands of mammals it may be assumed that relatively little secretion of style substance would occur in an absence of oxygen. Berkeley's work is open also to the objection that nowhere does he mention having watched his molluscs to determine whether they opened up and siphoned in the anaërobic water. Such observations are imperative owing to "sulking" on the part of some bivalves after handling, even when the surrounding water is plentifully supplied with oxygen and food. I find that the oyster will not open in oxygen-free water until it becomes too weak to remain closed. Dissolution of the style occurs when many species of bivalves remain tightly closed for a few hours, irrespective of whether the surrounding water is aërated.

In connection with the relation between the degree of aëration of natural waters and style formation it is of interest to compare the crystalline style of *Pisidium idahoense* with that of *Mactra*. *Pisidium* occurs in abundance in the mud at the bottom of Lake Mendota, Wisconsin, where for two thirds of the year the water may be completely devoid of oxygen (Birge and Juday, '11, Cole, '21). *Mactra* on the other hand lives in or close to the breaker line along sandy coasts, where the water at all seasons of the year is saturated with oxygen. The style of *Pisidium* is no larger than that of other Cyrenidæ which live in relatively well aërated creeks and ponds, whereas the crystalline styles of all *Mactra* which I have examined are relatively large, firm, and among the best developed of the styles I have found in any bivalve.

In *Ostrea* the direct relationship of crystalline style secretion to feeding can readily be demonstrated since this process assumes a somewhat rhythmic character. During the flood tide when the bivalves are feeding actively the style is large and firm, but by the late ebb tide, at which time most of the sand has been sorted out and removed from the stomach and digestion is well under way, the style may be reduced to a soft amorphous mass of jelly. The crystalline style is usually thin or entirely lacking at sunrise before active feeding of the molluscs has commenced. I agree therefore with Berkeley that his conception of the respiratory function of the crystalline style rests upon insecure evidence; and I believe that this theory, interesting though it be, must be added to the long list of the purely suppositious functions of the style which have been proposed during the past two hundred and thirty years.

Bökmann ('23) figures the crystalline style and the style sac of *Mytilus chorus* and his account agrees with the conclusions of List and of Mitra. From a histological study of the ciliated epithelium of the style sac he concluded that this must serve to put the style in rotation, although he did not observe the movement. This author apparently was not familiar with the work of recent American investigators.

A paper of much interest and valuable for its collection of many observations under one head is that of Yonge ('23) in which for the first time is given in one place an adequate account of the mechanisms of feeding and of digestion in a bivalve mollusc. This investigator traces the fate of food particles from the time they enter the incurrent siphon until the waste is expelled from the anus. No new information regarding the function of the style is given in this paper, but the recent literature is well summarized and a clear description is given of the rôle of the crystalline style in digestion in *Mya*. A study is made of the effects of varying concentrations of enzyme and of substrate, using the style and starch solutions. The optimum temperature for the reaction was found to lie at approximately 32° C., with complete destruction of the enzyme at 51° C. From the data thus collected it is concluded that the powerful amylolytic ferment of the style of *Mya* shows all of the characteristic properties of such an enzyme.

It is pointed out that the lamellibranchs may be arranged into taxonomic groups on the basis of the morphology of the style sac and intestine, but that such a grouping does not follow the modern classification based on the gill structure. Yonge considers that either our present system of classification is faulty or that independent evolution has occurred within the digestive system. I believe the latter to be the case since the morphology of the digestive tract is to a high degree correlated with the food habits and the habitat of the molluscs. This aspect of the problem is discussed likewise by Robson ('22) for the style sac and intestine of gastropods as well as of lamellibranchs.

Criticisms of Yonge's work are, first, his failure to consider the important rôle of the leucocytes in digestion, especially of fat;[1] and second, an inadequate appreciation of the part played by the hepatopancreas in the digestion and absorption of food as demonstrated by List ('02). From microscopic examinations of this organ during the later stages of digestion in *Ostrea* and especially in *Modiolus* I am led to believe that in these forms even more food is digested in the hepatopancreas than in the stomach. I believe the functions of the stomach, in some lamellibranchs at least, to be chiefly those of sorting over of food materials and the final separation of dirt, and of mixing food and enzymes, rather than those of an organ where complete digestion is effected.

Lazier ('24) in a valuable paper on the morphology of the digestive tract of *Teredo navalis* confirms for *Teredo* the conclusions of my 1918 paper regarding the origin and function of the crystalline style. His investigation of the morphology of the stomach, style-sac, and intestine shows that these structures are essentially similar to those of other molluscs in which the style-sac is completely separated from the intestine. The style of *Teredo* is believed to be rotated in the manner I described for *Modiolus*, and in *Anodonta*, although the actual rotation was not observed by Lazier.

In some of the marine borers, however, (*Pholas* and *Martesia* for example) the style is of such proportions that if rotation occurs it must be very slow. In my 1918 paper is figured a transverse section of *Martesia* showing a style of a mass approximately equivalent to the entire remainder of the body exclusive of the gills. This aspect of the problem needs further investigation, especially as to the part played by the style in the acquisition and possible sorting over of the borings ingested by *Teredo* and its wood-boring allies.

Churchill and Lewis ('24) make a valuable contribution to our knowledge of the mechanism of feeding in young bivalves. No

[1] A recent paper by Vonk '24 gives a good summary of the work in this field and adds some original observations.

new data are given regarding the nature of use of the crystalline style, the authors accepting the conclusions of my 1918 paper.

In conclusion it is apparent that the main facts regarding the origin, nature, and function of the crystalline style may be considered as quite firmly established and that we are now in a position to attack with the aid of modern methods and the newer knowledge of general physiology some of the problems of nutrition in molluscs.

Summary.

The period of 74 days required for style reformation in *Mya* as determined by Edmondson ('20) represents not only the time during which a new style is regenerating after extraction, but also the period of recovery following the rather drastic operation performed by this investigator. From data procured from other species of lamellibranchs it would appear that the time necessary for actual reformation of the style is much less than the figure given.

It was shown (Nelson, '18) that owing to the imperfect mode of separation of food particles from dirt and sand in the stomach of bivalve molluscs, some undigested food materials may escape down the intestine. In those forms in which the style sac is incompletely separated from the intestine a part of this rejected food material may be incorporated into the crystalline style, thus eventually being returned to the stomach. The remainder pass out undigested in the fæces. Failure to recognize this fact has led at least two recent investigators to conclude that such living organisms as are recovered from the fæces cannot be utilized by the molluscs as food.

The degree of solidity and of resistance to dissolution of the crystalline style are suggested by Nogouchi ('21) as factors controlling the presence or absence of Cristispira. That the solidity and the resistance of the style are not the primary factors involved in the distribution of Cristispira is shown by the presence of these spirochætes in the styles of *Ostrea* and of *Mya* which represent respectively minimum and maximum hardness.

Martin ('23) showed that a style may arise in *Ostrea* as a direct response to siphoning in aërated water even when the incoming water is devoid of all net and nannoplankton or other sources of

food. Berkeley ('23) found no style reformation under anaërobic conditions. His conclusion, however, that the style represents a reserve of oxygen is open to serious objection as herein explained.

The conclusions of Edmondson, '20, Allen, '21, Coker and others, '21, Bökman, '23, Churchill and Lewis, '24, and of Lazier, '24, agree in confirming the work of Coupin, '00, and the conclusions of my 1918 paper. Except in so far as the latter are modified by the findings of Martin and of Berkeley, as set forth in this paper, it is believed that the conclusions of Coupin and of the writer represent the consensus of opinion today regarding the origin, nature, and function of the crystalline style of lamellibranch molluscs.

Citations.

Allen, W. R.

'14 The Food and Feeding Nabits of Fresh-water Mussels. Biol. Bull., 27, 127–139.

'21 Studies of the Biology of Fresh-water Mussels. Experimental Studies of the Food Relations of Certain Unionidæ. Biol. Bull., 40, 210–241.

Berkeley, C.

'23 On the Crystalline Style as a Possible Factor in the Anaërobic Respiration of Certain Marine Molluscs. J. Exp. Zoöl., 37, 477–488.

Vonk, H. J.

'24 Verdauungsphagocytose bei den austern. Zeitschr. f. vergl. Physiol. Bd. 1, H. 3, 4.

Birge E. A., and Juday, C.

'11 The Inland Lakes of Wisconsin. The Dissolved Gases of the Water and their Biological Significance. Bull Wis. Geol. and Nat. Hist. Sur., 22, p. x + 259.

Blegvad, H.

'15 Food and Conditions of Nourishment among the Communities of Invertebrate Animals Found on or in the Sea Bottom in Danish Waters. Rept. Dan. Biol. Sta. for 1914, 22, 41–78.

Bökman, F.

'23 Ueber Stoffwechselorgane einiger Mytiliden. Jen. Zeit. f. Naturwiss. 59, 209–260.

Churchill, E. P., and Lewis, S. I.

'24 Food and Feeding of Fresh-water Mussels. Bull. U. S. B. F. 39, 439–471.

Coker, R. E., Shira, A. F., Clark, H. W., and Howard, A. D.

'21 Natural History and Propagation of Fresh-water Mussels. Bull. U. S. B. F.

Cole, A. E.

'21 Oxygen Supply of Certain Animals Living in Water Containing No Dissolved Oxygen. J. Exp. Zoöl., 33, 239–320.

Collip, J. B.

'20 Studies on Molluskan Cœlomic Fluid. Effect of Change of Environment on the Carbon Dioxide Content of the Cœlomic Fluid. Anaërobic Respiration in *Mya arenaria*. J. Biol. Chem., 45, 23–49.

'21 A Further Study of the Respiratory Processes in *Mya arenaria* and other Marine Mollusca. J. Biol. Chem., 49, 297–310.

Edmondson, C. H.

'20 The Reformation of the Crystalline Style in *Mya arenaria* after extraction. J. Exp. Zoöl., 30, 259–291.

Gray, J.

'23 The Mechanism of Ciliary Movement. III. The Effect of Temperature. Proc. Roy. Soc., 95, Ser. B, No. B664, 6–15.

Lazier, E. L.

'24 Morphology of the Digestive Tract of *Teredo navalis*. U. of Cal. Publ. Zoöl., 22, 455–474.

Martin, G. W.

'23 Food of the Oyster. Bot. Gaz., 75, 143–169.

Nelson, T. C.

'18 On the Origin, Nature, and Function of the Crystalline Style of Lamellibranchs. J. Morph., 31, 53–111.

Nogouchi, H.

'21 Cristispira in North American Shellfish. J. Exp. Med., 34, 299–315.

Robson, G. C.

'22 On the Style Sac and Intestine in Gastropoda and Lamellibranchia. Proc. Malacal. Soc., 15.

Yonge, C. M.

'23 Studies on the Comparative Physiology of Digestion. 1. The Mechanism of Feeding, Digestion, and Assimilation in the Lamellibranch *Mya*. Brit. J. Exp. Biol., 1, 15–63.